Swimming Speed and Oxygen Consumption in the Bathypelagic Mysid *Gnathophausia ingens*

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Abstract. The energetic costs of swimming were determined for the bathypelagic mysid *Gnathophausia ingens.* Individuals over a large size range spontaneously swam at speeds from 5 to 6.5 cm/s. To maintain this speed, smaller animals swam at much higher relative swimming speeds than did larger animals. Routine rates of oxygen consumption were thus considerably higher in the smaller instars. The relationship between standard rates of oxygen consumption and animal size was slightly less than the standard log-log allometric slope of 0.75. Within the speed range of 0–8 cm/s, oxygen consumption appeared to increase as a linear function of speed. Cost of transport was very high at low speeds. At 5.5 cm/s, cost of transport was lower than that measured for other crustaceans, but higher than that of fish. Swimming efficiency increased with speed. While the lower cost of transport and higher swimming efficiency may contribute to *G. ingens'* reduced rates of oxygen consumption as compared to those of shallower-living crustaceans, the major factor appears to be *G. ingens'* lower level of swimming activity.

Introduction

It is well known that deep-living pelagic fish and crustaceans have metabolic rates considerably lower than those of shallower-living pelagic species (Childress, 1969, 1971b, 1975, 1977; Smith and Hessler, 1974; Torres *et al.,* 1979; Smith, 1978; Smith and Laver, 1981; Cowles, 1987). This reduction is of an order of magnitude or more, and can be only partially accounted for by changes in temperature, pressure, and animal protein content with depth (Childress, 1975; Mickel and Childress, 1982). Lower metabolic rates at depth have generally been attributed to selection for energy conservation due

to food limitation at depth (Childress and Nygaard, 1973, 1974; Bailey and Robison, 1986). A more recent hypothesis contends that, for deeper-living animals such as fish and crustaceans which rely on vision for detection of predators or prey, the reduction in metabolic rate is related to a decrease in activity and the capacity for activity, which is allowed by the shorter reactive distances at depth and consequent relaxation of selection for capacities for rapid swimming (Childress *et al.,* 1980; Childress and Mickel, 1985).

For any active pelagic species, locomotory activity may be expected to play a prominent role in determining the overall metabolic rate. Activity may be critical for feeding, escape from predation, vertical migrations, finding a mate, and maintaining station in the water column. However, little is known of the normal activity levels of deep-living pelagic crustaceans nor of the amount of metabolic energy such activity requires. A few studies have been made on swimming speeds and rates of aerobic metabolism of shallow-living pelagic crustaceans. Torres *et al.* (1982) and Torres and Childress (1983) used an annular chamber to measure swimming activity and rate of oxygen consumption in the shallow-living *Euphausia pacifica.* Kils (1979a, b) measured mean rates of oxygen consumption and recorded average swimming speeds for the Antarctic krill, *Euphausia superba.* No comparable data, however, are available for deep-living crustaceans. Mickel and Childress (1978, 1982) and Quetin and Childress (1980) measured pleopod beat rates and oxygen consumption in the mysid *Gnathophausia ingens* strapped to a fixed underwater frame. It is not clear, however, what correlation exists between pleopod beat rates and swimming speeds in swimming crustaceans.

Gnathophausia ingens Dohrn (1870) is a large cosmopolitan bathypelagic mysid from the family Lophogastri-

dae. The species is negatively buoyant in seawater and appears to be an active swimmer. Most of the population of this species off California live at depths of 400 to 900 meters (Childress, 1975). Since the species can be maintained in the laboratory for long periods of time, more has been learned about its physiology than that of nearly any other large pelagic crustacean (Childress, 1968, 1969, 1971b; Fuzessery and Childress, 1975; Belman and Childress, 1976; Childress and Price, 1978, 1983; Mickel and Childress, 1978, 1982; Quetin and Childress, 1980; Hiller-Adams and Childress, 1983a, b, c; Cowles, 1987). Like many deep-sea animals, its rate of aerobic metabolism is significantly lower than that of comparable epipelagic animals.

In this study we measured the relationship between routine swimming speeds and rates of oxygen consumption in *G. ingens*. These data were used to characterize energetic costs of swimming for this species. Swimming energetics of *G. ingens* were then compared to those of shallower-living crustaceans and of fish to evaluate *G. ingens'* relative swimming abilities and costs in comparison to those of other active pelagic swimmers.

Materials and Methods

Seventy-two *Gnathophausia ingens* of instars 5–11 (Childress and Price, 1978, 1983) were obtained from depths of 450–750 meters from San Clemente, Catalina, and Santa Cruz basins off Southern California, using a 10-foot square Tucker Trawl fitted with a thermally insulated cod end (Childress *et al.*, 1978). The mysids were maintained in the laboratory in 5.5°C seawater in 1-liter plastic containers and were fed once a week to satiation with an alternating diet of salmon and shrimp. Individuals kept in the laboratory were starved at least twenty-four hours before being used for an experiment. Length of stay in the laboratory before use in an experiment ranged from one hour to six months, with the majority being used within twenty days.

Swimming speed and rate of oxygen consumption were measured in a recirculating swim tunnel similar to that described by Cowles *et al.* (1986). Modifications included an increase in diameter to 10.16 cm, the total enclosure of the tunnel for respiration measurements, and the connection of the tunnel to a computer-based data acquisition and control system for continuous data logging. Ultraviolet sterilized, 0.2 μm filtered seawater containing 25 mg/l each of streptomycin and penicillin was used during oxygen consumption experiments to minimize background microbial respiration. A dark cover was placed over the chamber to minimize disturbance to the animal during the experiment.

Experimental animals were sealed individually in the swim tunnel and allowed to swim at spontaneous speeds while speed and oxygen consumption were measured continuously. Individual experiments varied in length from four to thirty hours. An experiment was terminated when it had proceeded long enough so that at least several hours of steady oxygen consumption data had been obtained, preferably at a range of speeds. The animal was then removed, weighed wet, and returned to a holding tank of chilled seawater. Later the live, anesthetized animal's underwater weight was determined in 5.5°C seawater, and the animal was dried to determine dry mass.

Data obtained from the swim tunnel were used to calculate rate of oxygen consumption [MO_2, micromoles O_2/ (mg wet wt × h)] as a function of absolute (S_a, cm/s) and relative (S_r, lengths/s) for each mysid. The mean absolute (S_{mar}) and relative (S_{mrr}) swimming speeds and rate of oxygen consumption (MO_{2mr}) for the entire session in the swim tunnel were calculated for each mysid, with the assumption that these speeds, swum spontaneously by the mysid, represent routine swimming speeds. In addition, the maximum swimming speed maintained for at least one minute, identified as the maximum short-term swimming speed, was noted for each individual.

Data for all animals from each instar were grouped together, and the mean S_{mar}, S_{mrr}, MO_{2mr}, and wet, dry, and underwater weights were calculated for each instar. Best fit mean-square linear and power regressions for the relationship between S_{mar}, S_{mrr} and MO_{2mr} were calculated for each instar and for all the instars combined. Swimming speeds and rates of oxygen consumption for each instar were compared by analysis of variance and by a regression of these variables against carapace length. The best-fit equation relating rate of oxygen consumption (MO_2) to swimming speed (S_a) and body mass (grams wet weight) was determined by least squares multiple regression. All references to statistical significance in these experiments were based on the 95% confidence level. References to rates of oxygen consumption conform to the terminology conventions of Piiper *et al.* (1971).

Results

Swimming speeds and rates of oxygen consumption

Upon first being placed in the swim tunnel, many of the animals swam rapidly and erratically for some time. Maximum short-term speeds were usually recorded during this early period (Table I). Maximum short-term speeds varied from 10.3 to 18.2 centimeters per second (1 length per second for the larger instars, 2 lengths per second for the smaller).

After this initial acclimation period of one to three hours, most individuals swam at a characteristic speed that varied little throughout the rest of the experiment.

Table I

Swimming speeds and rates of oxygen consumption of Gnathophausia ingens *maintained in the laboratory for less than 30 days, by instar*

| Instar | n | Mean weight (g) | | | Mean length | | Swimming speed* | | | | | | Rate of oxygen consumption | |
| | | | | | | | Mean | | | | Maximum cm/s | | | |
		Wet	Dry	Under water	Carapace mm	Total cm	S_{mar} cm/s	s.d.	S_{mrr} length/s	s.d.	Short	Sustained	MO_{2mrr}#	s.d.
5	7	0.718	0.114	0.015	15.9	5.2	3.5	2.6	0.67	0.49	10.3	7.5	0.0125	0.00943
6	13	1.27	0.260	0.021	20.2	6.2	5.8	1.7	0.93	0.27	12.8	8.6	0.0116	0.00811
7	14	2.22	0.382	0.030	24.3	7.2	6.2	2.3	0.86	0.32	15.4	10.3	0.00575	0.00307
8	13	4.07	0.772	0.047	30.0	8.5	6.3	2.2	0.74	0.26	18.2	11.6	0.00453	0.00229
9	10	7.12	1.321	0.086	35.9	9.9	5.1	1.1	0.51	0.10	18.2	12.2	0.00271	0.00172
5–9	72	3.10	0.472	0.040	25.6	7.5	5.6	2.1	0.76	0.32	18.2	12.2	0.00725	0.00641

* Mean speeds are the average swimming speeds of all individuals of the instar combined. Maximum "short" speeds are the highest speeds maintained by any individual of the instar for 1 minute; maximum sustained speeds are the highest speeds sustained by any individual in the instar for at least 20 minutes.

MO_2 units = micromoles O_2/(mg wet wt $\times$ h).

No significant differences in swimming speed between day and night were observed. Swimming speed and the accompanying rates of oxygen consumption were significantly lower for animals that had been maintained in the laboratory for thirty days or longer ($P < .005$ and .0002, respectively). Mean routine swimming speeds (S_{mar}, cm/s) and rates of oxygen consumption [MO_{2mr}, micromoles O_2/ (mg wet wt $\times$ h)] for each instar are summarized in Table I. This table contains data for only those animals that had been in the laboratory for less than thirty days. Except for the smallest individuals (instar 5), routine absolute swimming speed averaged around 5 to 6.5 cm/s for all animals, regardless of instar. Instar 5 animals swam significantly more slowly than the other instars ($P < .05$), but there was no significant difference in absolute swimming speeds among instars 6 through 9 (Fig. 1A). The slope of a regression of S_{mar} *versus* animal length for instars 6 through 9 was not significantly different from zero ($P = .52$).

Significant trends in mean relative routine swimming speeds (S_{mrr}) were found among the instars. The relative routine swimming speeds of each of the instars 6 through 8 were significantly higher than those of all larger instars. A regression of S_{mrr} *versus* animal length for instars 6 through 9 had a highly significant downward trend ($P < .001$), indicating the slower relative swimming speeds of the larger instars. Most instar 5 animals swam at a slower relative speed than predicted by this regression, but faster than the largest instars (Fig. 1B).

The body angle of the swimming mysids changed with swimming speed. At low speeds the body angled upward anteriorly, becoming more horizontal as speed increased. For any given absolute swimming speed, body angle was greater for the smaller instars. By 8 cm/s the

body was essentially horizontal. This trend is similar to that reported by Kils (1979b) for swimming *Euphausia superba*, and that reported by Cowles *et al.* (1986) for passive body movements of dead *G. ingens*.

In the animals for which pleopod beat rate was recorded, no significant relationship was found between pleopod beat rate and swimming speed within the narrow range of swimming speeds observed. The pleopods beat at around 150–230 strokes per minute, regardless of swimming speed. The relationship between pleopod beat rate, swimming speed, and body angle for one individual is shown in Figure 2.

Significant differences in rates of oxygen consumption were measured between instars. With the exception of instar 5, routine mass-specific metabolic rates (MO_{2mr}) were significantly higher for the smaller instars than for larger ones (Fig. 1C).

Most individual animals swam at a typical speed for that individual, with little deviation throughout the experiment. The maximum sustained speed, defined as the highest swimming speed maintained for at least 20 minutes, recorded for any animal of a particular instar was typically less than twice the average swimming speed of individuals from that instar. Few animals swam at a large enough range of speeds to determine the relationship between swimming speed and rate of oxygen consumption. In those that did, the relationship was approximately linear (Fig. 3).

The best-fit equation relating rate of oxygen consumption (MO_2) to swimming speed (S_a) and body mass (g wet wt) was:

$$MO_2 = 0.00289 - 0.00216 \log_{10} g + 0.00156 S_a$$
$$- 0.00167 (\log_{10} g) \times S_a \quad (1)$$
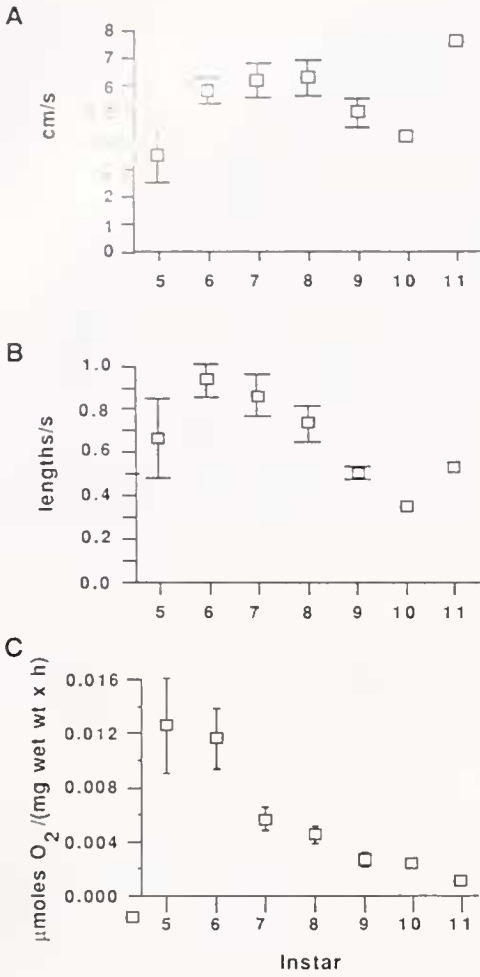
Figure 1. A. Mean swimming speeds, in centimeters per second, for each instar. B. Mean swimming speeds, in lengths per second, for each instar. C. Mass-specific routine oxygen consumption rates, in micromoles of oxygen per milligram wet mass per hour, for each instar in swim tunnel. Error bars are standard error.

$(R^2 = 0.45$, Standard error of estimate 0.00456, P slope $= 0 \ll .001)$

The increase in MO_2 with increase in relative swimming speed (S_r) was approximately the same for each instar, increasing by an amount equal to the standard rate of aerobic metabolism for each 0.1 to 0.25 length per second increase in speed.

Animal size and rates of oxygen consumption

For any given absolute swimming speed, MO_{2mr} of the smaller instars was higher than that of the larger instars (Fig. 4). This effect was reduced but not eliminated by converting swimming speeds to lengths per second for each instar. The smaller animals thus had higher rates of oxygen consumption than did the larger animals at any given swimming speed.
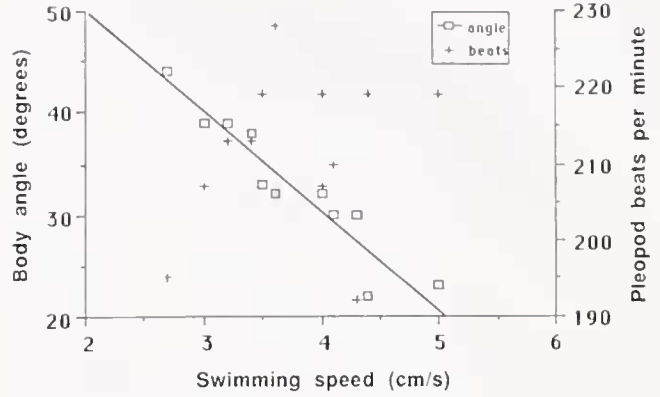

Figure 2. The relationship between swimming speed, body angle, and pleopod beat rate for one instar 6 *Gnathophausia ingens*. Body angle from horizontal (squares) decreases significantly with swimming speed ($P < .001$). There is no significant correlation between pleopod beat rate (crosses) and swimming speed.

The best-fit allometric equation relating mean standard total rate of oxygen consumption (MO_{2tms}, micromoles O_2/h), as calculated using equation 1, to animal wet mass (WWT, grams) was:

$$MO_{2tms} = 2.76 \; WWT^{0.547 \pm 0.179} \qquad (2)$$

The fact that the smaller instars spontaneously swam at higher relative speeds than did the larger instars led to an allometric relationship between wet mass and mean routine total rate of oxygen consumption (MO_{2tmr}) which was significantly different from the relationship between wet mass and standard oxygen consumption. The best-fit equation for routine rates of oxygen consumption was:

$$MO_{2tmr} = 8.28 \; WWT^{0.307 \pm .238} \qquad (3)$$
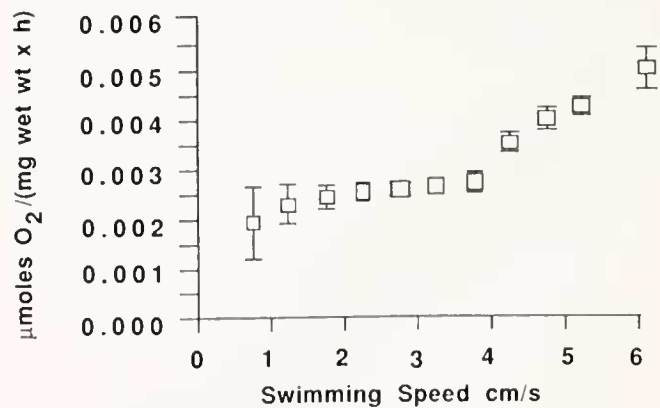
Figure 3. Relationship of swimming speed (X, cm/s) to rate of oxygen consumption (Y, micromoles $O_2/$ (mg wet wt × h) for one *Gnathophausia ingens*. Error bars are standard deviation.

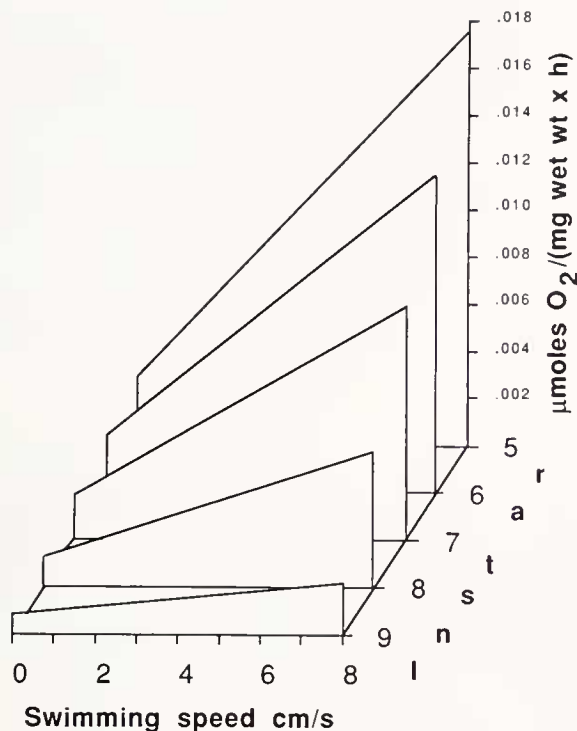**Figure 4.** A comparison of the best-fit linear regressions of mass-specific rate of oxygen consumption [micromoles O_2/ (mg wet wt × h)] as a function of absolute swimming speed (cm/s) for *Gnathophausia ingens* instars 5-9, based on equation 1.

Discussion

Swimming speeds

Comparison of *G. ingens'* routine swimming speed of 5 to 6.5 centimeters per second (0.5 to 1 body length per second) to that of other, shallower-living pelagic crustaceans is difficult, since few comparable measurements have been reported (Table II). All shallow-living species cited are smaller than the deep-living *G. ingens* but swim at faster relative speeds. *G. ingens* is also capable of swimming much faster than its routine speeds, as demonstrated by several animals that swam at over 18 cm/s

(over 2 lengths/s) for several minutes when first introduced to the swim chamber, and by the maximum sustained speeds of 7.5–12.2 centimeters per second (1–1.5 lengths/s) (Table I). However, these relative speeds for *G. ingens* are as little as one tenth that of the shallower-living species when the difference in body length is taken into account. If the highest speeds cited above for each species are taken as an estimate of the animals' burst speeds, *G. ingens'* burst speeds are also markedly lower than those of shallower-living pelagic crustaceans.

To attain the routine swimming speeds of 5 to 6.5 cm/s, the swimming speed of most *G. ingens* instars, the smaller instars had to swim at relative speeds of nearly twice as many body lengths per second as compared to the larger instars. The routine swimming speeds of the smaller instars thus approached more closely to their maximum sustained speeds (Table I). This may be why the absolute swimming speeds of instar 5 animals were somewhat lower than those of most of the larger instars. If instar 5 animals were to swim at 5 to 6.5 centimeters per second, as the larger instars did, they would be swimming at 1 to 1.25 lengths/s, or nearly the maximum sustained relative speed (1.4 lengths/s) attained by any instar.

Swimming speeds and rates of aerobic metabolism

Due to the relatively restricted range of routine swimming speeds selected by *G. ingens* in this experiment, it was not possible to determine conclusively the shape of the relationship between swimming velocity and rate of oxygen consumption. However, several lines of evidence indicate that the relationship is linear over the limited range of speeds studied. In the few animals that swam at a wide range of speeds, the relationship between velocity and rate of oxygen consumption appeared to be approximately linear, as shown in Figure 3. When data from all individuals of a given instar were pooled, the best-fit relationship in each instar measured was linear over the range of speeds tested. Stepwise linear regression indicated that rate of oxygen consumption was related directly to swimming speed, and not to the logarithm nor

Table II

Comparison of crustacean swimming speeds reported in the literature

Species	Length (cm)	cm/s	Lengths/s	Reference
Gnathophausia ingens	5.2–9.9	5.0–6.5	0.5–1	This paper
Euphausia superba	4–5	5.6	1.25	Kils (1979a)
Mysis relicta	3	5–10	2–3	Robertson *et al.* (1968)
Neomysis americana	11.4	6–8	5–7	Hargreaves (1981)
	0.6–1.7	3–10	5–6	Hargreaves (1981)
Acanthomysis sp.	0.7	9–10	10–14	Allen (1978)
Mysidium columbiae		20		Steven (1961)

to the square of speed. In addition, Cowles *et al.* (1986) showed that drag on a dead mysid's body increases linearly with velocity over the speed range at which these animals were swimming. Since thrust in a steadily swimming animal is equal to drag (Wu, 1977), thrust and metabolic energy consumption would also increase linearly with swimming speed in these animals if drag on a dead mysid is representative of drag on a live, swimming mysid.

A linear relationship between swimming velocity and rate of oxygen consumption has also been reported for several other crustacean species. Halcrow and Boyd, (1967) found a linear relationship for the amphipod *Gammarus oceanicus*, as did Torres and Childress, (1983) for *Euphausia pacifica*. A number of other crustaceans, however, have been found to have nonlinear relationships between swimming velocity and rate of oxygen consumption. The basis for these differences is not clear. However, it appears likely that at higher speeds the relationship between velocity and oxygen consumption in *G. ingens* would begin to conform more closely to an exponential relationship (Hargreaves, 1981; Webb, 1975a; Cowles *et al.*, 1986).

Size dependency of oxygen consumption

It has been shown for numerous organisms that the slope of the allometric equation of the logarithm of total oxygen consumed (Y) *versus* the logarithm of the animal's mass (X) generally falls in the range of 0.67 to 1, usually being about 0.75 (Kleiber, 1947; Wolvekamp and Waterman, 1960; Wu, 1977; Schmidt-Nielsen, 1979). This relationship holds for standard or basal metabolism (Winberg, 1956, 1961; Hemmingsen, 1960; Brett, 1965; Brett and Glass, 1973; Wilkie, 1977; Peters, 1983), for routine metabolism (Job, 1957), and for active metabolism (Brett, 1965; Brett and Glass, 1973; Taylor *et al.*, 1981; Prothero, 1979). Childress (1971a) and Hiller-Adams and Childress (1983c) found a similar relationship between animal size and routine oxygen consumption in *G. ingens*. The standard rates of aerobic metabolism determined in this study were generally lower than these rates (Fig. 5). The routine rates of oxygen consumption reported by Childress (1971a) and Hiller-Adams and Childress (1983c) were similar to rates associated with swimming speeds of 0.25 lengths/s in this study.

Though the slope of the allometric relationship between size and standard metabolic rate (equation 2) was lower than the 0.75 generally found for such relationships, the difference was barely significant. On the other hand, the slope of the allometric regression of the animals' routine metabolic rates *versus* wet mass was highly significantly less than 0.75 (equation 3), and for the
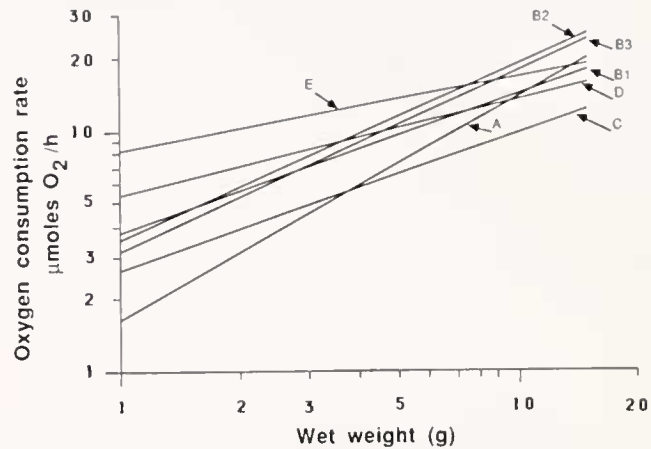

Figure 5. A comparison of the best-fit least-squares linear regressions of the allometric relationship between total rate of oxygen consumption (Y, micromoles O_2/h) *versus* wet mass (X, grams), from several studies of *Gnathophausia ingens'* oxygen consumption rate. Lines: A: from Childress (1971). B1–B3: from Hiller-Adams and Childress (1983c). C to E: rates of oxygen consumption as measured in this study. C: standard rate (0 cm/s). D: oxygen consumption rate at 0.25 lengths per second swimming speed. E: routine oxygen consumption rates.

smaller instars the rates of oxygen consumption were significantly higher than those previously reported for *G. ingens* (Fig. 5). This trend reflects the higher relative swimming speeds and rates of oxygen consumption of the smaller instars under the conditions of the swim tunnel. In this experiment, the animals swam freely in the tunnel at a speed they set themselves, restrained only by connection to a movable force transducer. In previous reports (Childress, 1971a; Hiller-Adams and Childress, 1983c), oxygen consumption was measured within a small enclosed respiration chamber in which the animals lay, beating their pleopods. Since these animals were free to set their own pleopod beat rates within the confines of the chamber, it may be assumed that the rates of oxygen consumption measured under these conditions were routine rates. The fact that the slopes of the allometric relationships obtained under these conditions were similar to the expected slopes of 0.75 supports this assumption. However, in light of the data obtained in the present study, it appears that the definition of routine activity as applied to active, negatively buoyant crustaceans such as *G. ingens* needs to be refined. It appears that the animals in the enclosed chambers, which were not free to swim about, assumed a uniform level of activity that was similar in all instars and equivalent to a swimming speed of approximately 0.25 lengths per second. The present experiment shows that when free to swim through the water, however, the smaller instars assume a much higher level of spontaneous activity than the larger instars do. "Routine" activity levels are markedly different for the different instars if the animal is in a free-swim-

ming state, as in this experiment, but not if the animal is not free to swim about, as in the Childress (1971a) and Hiller-Adams and Childress (1983c) experiments. If one is interested in comparing rates of oxygen consumption at some standard level of activity, then the rates measured by Childress (1971a) and Hiller-Adams and Childress (1983c) will do. However, this study shows that if one is estimating actual energy expenditures as may occur under routine conditions in the field, one must account for the different levels of routine activity the different instars assume when left to swim freely.

Cost of transport

The energy expenditure of an actively moving animal can be described in terms of cost of transport, or the amount of energy required to move a given distance through the medium. Cost of transport is influenced by a number of variables including speed, mode of transport, animal size and shape, and medium. For calculating cost of transport, the linear relationship between swimming speed and rate of oxygen consumption was recalculated in terms of energy expended per unit distance [calories/(g × km)]. A respiratory quotient (RQ) of 0.79 was used, reflecting metabolism of a mixture of carbohydrate, protein, and fat (Bartholomew, 1977). When this RQ is used, 1 micromole of oxygen is equivalent to 0.1075 calories. Instar 8 was selected as an average animal for cost of transport estimation. Instar 8 animals weighed an average of 4.07 grams, and the relationship between speed and rate of oxygen consumption is given in equation 1. Using these data, this animal's energy expenditure per unit distance (CT, calories per gram-kilometer) [cal/(g × km)] while swimming is:

$$CT = 1.63 \left(\frac{3.87}{S_a} + 1 \right) \tag{4}$$

This relationship is shown graphically in Figure 6. As can be seen, the energy required per unit distance is very high for low swimming speeds, dropping rapidly with increasing speed at low speeds and then much more gradually at speeds above 3 cm/s. This relationship makes it clear that, for *G. ingens,* lowest costs of transport per unit distance are incurred at speeds above 3 cm/s. This fits well with the empirical observation that these mysids swim at a characteristic speed of 5 to 6.5 cm/s. Slower swimming speeds would be energetically expensive, entailing a high cost per unit distance. On the other hand, equation 4 predicts that swimming faster than 5 or 6 cm/s would at best result in only minimal reduction in cost of transport. In reality, higher swimming speeds are likely to result in even higher costs than predicted, due to increasing turbulence and to the exponential increase in drag with speed predicted by hydrodynamic equations
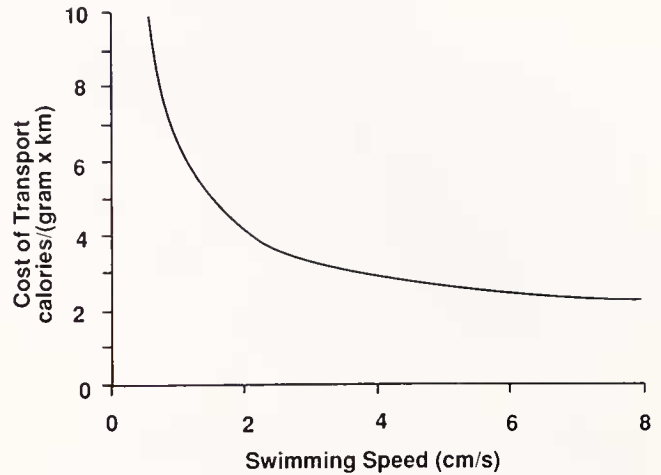

Figure 6. Cost of transport (CT, calories per gram-kilometer) as a function of swimming speed (S_a, cm/s) for *Gnathophausia ingens* of instar 8. Equation: $CT = 1.63 [(3.87/S_a) + 1]$

(Webb, 1975a). Over the 0 to 8 cm/s range of swimming speeds measured in this experiment, change in body angle with speed appears to mask these effects, but at higher speeds they can be expected to become more prominent, resulting in an increase in cost of transport at higher speeds.

In terms of energy expenditure per unit time, higher swimming speeds also have higher costs due to the increase in metabolic rate with speed. *G. ingens'* routine swimming speeds thus appear to be intermediate between the very low speeds, with their high costs of transport per unit distance, and very high speeds, with their high metabolic costs per unit time and distance.

At a speed of 5.5 cm/s, a 4.07 gram *G. ingens* would have a cost of transport of 2.78 cal/(g × km), or 11.3 cal/km. This value is slightly higher than values estimated from the regression lines shown in Schmidt-Nielsen, (1972) Tucker, (1975), Beamish, (1978), and Hargreaves, (1981), all of which are for swimming fish. None of these authors state the equation for their regression lines; however, Schmidt-Nielsen's data are calculated from data given by Brett (1965) for swimming sockeye salmon of 3.38 to 1432 grams. A regression of Brett's data (for salmon in 15°C water), converted to the units of equation 4, is:

$$CT = 2.05 \, WWT^{-0.254 \pm 0.054} \tag{5}$$

A 4.07 gram *G. ingens* swimming at 5.5 cm/s would have a cost of transport of 2.78 cal/(g × km), while the above equation predicts that cost of transport for a fish of the same size would be 1.43 cal/(g × km).

Torres (1984), using data from Brett and Glass (1973) for a size range of sockeye salmon, calculated net cost of transport for swimming fish. Torres' equation is:

$$CT_n = 1.416 \, WWT^{-0.25} \qquad (6)$$

(CT_n in this equation is net cost of transport [cal/(g $\times$ km)], therefore standard metabolic rate must be subtracted from the active metabolic rate before using this equation.) While this equation is based on salmon data, Torres has shown that the cost of transport of a number of other fish species falls near this line as well. For an instar 8 *G. ingens* swimming at 5.5 cm/s, the net cost of transport would be 1.82 cal/(g $\times$ km), while the value Torres' equation predicts for a fish of similar size is 0.997. *G. ingens'* cost of transport thus appears to be twice as high as that of fish of similar size. This trend has been noted for other crustaceans as well. Torres (1984) compiled net cost of transport data for a number of crustacean species and calculated an equation for crustacean net cost of transport analogous to equation 6. For crustaceans Torres' best-fit regression is:

$$CT_n = 6.26 \, WWT^{-0.28} \qquad (7)$$

This equation predicts a net cost of transport for a 4.07 gram crustacean swimming at 5.5 cm/s of 4.23 cal/(g $\times$ km), twice as high as the 1.82 calculated for *G. ingens*. Thus, *Gnathophausia ingens'* net cost of transport appears to be relatively low for crustaceans, which use paddle propulsion, but is higher than that for fish, which use an undulatory propulsion mode.

Swimming efficiency

Swimming efficiency, the ratio of the mechanical power required to overcome the drag an animal experiences while swimming to the metabolic power the animal uses for swimming, is a useful way to compare the efficiency of different propulsive mechanisms. Swimming efficiency has been determined for a number of fish, including salmon (Osborne, 1961; Webb, 1973, 1975a) and trout (Webb, 1971a, b), which swim in the subcarangiform mode, and *Cymatogaster aggregata* (Webb, 1975b) and goldfish (Smit, 1965, Smit *et al.*, 1971), which use pectoral fin propulsion. Calculated swimming efficiencies for the subcarangiform swimmers were low at low speeds, increasing to 15.8% at critical swimming speeds for trout and to 26% for salmon. Efficiency for *Cymatogaster aggregata* at critical swimming speed was 9.2 to 14%. Efficiency tends to increase with fish size and swimming speed (Webb, 1975a), and appears to be higher for the subcarangiform mode than for pectoral fin propulsion.

Previous studies of swimming efficiency in hard-bodied organisms such as crustaceans have mainly been estimates based on what is known about muscle efficiency and efficiency in fish. Klyashtorin and Yarzhombek (1973) used various efficiencies cited in the literature for ATP conversion, muscle efficiency, and paddle propulsion efficiency to arrive at an estimate of 5% for crustacean swimming efficiency. Hargreaves (1981) used similar calculations, along with the fish swimming efficiencies cited above, to estimate crustacean swimming efficiency at 10%. Nachtigall (1977) used a swimming efficiency of 10% for swimming water beetles, based in part on a calculation of 30% efficiency for the rowing apparatus.

Torres (1984) made a more direct calculation of swimming efficiency in the euphausiid *E. pacifica* by measuring rate of oxygen consumption at various swimming speeds and comparing these values to estimated drag based on hydrodynamic formulas. On the basis of this partly empirical data, he calculated swimming efficiency to vary from 0.014% at 1 cm/s to 2.85% at 20 cm/s. If the animal's drag were higher than his estimates based on hydrodynamic formulas, then the animal's swimming efficiency would be correspondingly higher.

Swimming efficiency in *G. ingens* may be calculated based on oxygen consumption data from this experiment (equation 1) and on drag data from Cowles *et al.* (1986). For an instar 8 individual (carapace length 3.0 cm), swimming efficiency E_s is described by the equation:

$$E_s = 2.96 \times 10^{-3} \, (S_a) \qquad (8)$$

At a swimming speed of 5.5 cm/s, swimming efficiency would be 1.6 percent. This efficiency is higher than the 0.097 to 0.133% reported by Torres (1984) for *E. pacifica* swimming at this speed, but is below that reported for fish.

Equation 8 indicates that *G. ingens'* swimming efficiency increases linearly with speed. At 8 cm/s, efficiency for an instar 8 animal would be 2.4%. Swimming efficiency also increases with speed for fish (Webb, 1975a), and for *E. pacifica* (Torres, 1984), though not linearly. In fish, the increase in efficiency with speed is thought to be linked to changes in propeller and muscle efficiency. It is not known whether this is also true for *G. ingens*. Efficiency and the changes in efficiency with speed of the multiple-paddle mode of propulsion used by *G. ingens* and many other pelagic crustaceans have not been adequately studied. Kils (1979b) found that *Euphausia superba* changes many aspects of the pleopod stroke with increases in speed over the range of 0–15 cm/s, including increasing abduction of the protopodites, increasing degree of spreading of propulsive setae, holding pleopods closer to the body on the return stroke, directing the propulsive stroke more directly to the posterior, and bringing the whole body into a more nearly horizontal orientation. These adjustments result in changes in the flow direction and size of the wake and in increased swimming velocity. Change in pleopod beat rate is small over this entire range of speeds, increasing from 150 to 180 beats per minute. Increase in swimming speed is accom-

plished by a linear increase in the transport distance per beat rather than an increase in pleopod beat rate. *E. superba* thus appears to control swimming speed by modifying stroke efficiency at speeds up to 15 cm/s. At this speed maximum stroke efficiency appears to have been reached, and further increases in speed are brought about by changes in stroke rate. Mickel and Childress (1978) and Quetin and Childress (1980) observed that the pleopod beat rate of *G. ingens* strapped to a frame is remarkably constant, remaining at an average of between 140 and 210 beats per minute or stopping completely. *G. ingens* in the swim tunnel also maintained a similarly high, stable rate of pleopod beats, even with changes of swimming speed of at least a factor of two. It thus appears likely that *G. ingens* also adjusts swimming speed largely by changes in stroke characteristics, as does *E. superba*. Which parameters of the stroke are varied and how these changes contribute to stroke efficiency remain to be determined.

One likely factor influencing the increase in swimming efficiency in *G. ingens* with increasing speed is the change in body attitude (Fig. 2). At low speeds the animal swims with its body angled upward, directing a larger proportion of its thrust downward and thereby increasing lift. As speed increases, the body assumes a more horizontal orientation, so that a larger vector percentage of thrust is directed directly backward. This trend is likely to result in increasing efficiency in the generation of forward thrust with increasing speed, as observed. Eventually, however, the animal reaches a speed at which it assumes a nearly horizontal orientation in the water. The speed varies between instars, but by 8 cm/s most animals are nearly horizontal. This speed, at which increases in efficiency due to changes in body angle would be maximized, would correspond to an efficiency of 1.8% for *G. ingens* of instar 8.

Calculations for other instars, such as those carried out above for instar 8, indicate that swimming efficiency also increases with size in *G. ingens*. At 5.5 cm/s, efficiency for an instar 5 individual would be 0.8%, while that of an instar 9 individual would be 5.36%. Such a trend has also been noted for fish (Webb, 1975a).

Gnathophausia ingens *as a bathypelagic crustacean*

As an active pelagic crustacean, *G. ingens* appears to be more efficient and has lower costs of transport than shallower species, such as *E. pacifica*. However, the order of magnitude reduction in rate of oxygen consumption of the bathypelagic *G. ingens* can only be partially accounted for by these relatively small increases in swimming efficiency or reductions in cost of transport. The most obvious factor contributing to *G. ingens'* low rate of oxygen consumption is its reduced swimming speed

relative to surface-living crustaceans. *G. ingens'* routine relative swimming speeds are as low as one tenth those measured for shallower-living crustaceans, and its maximum speeds appear to be lower by the same factor. On the other hand, *G. ingens* is not inactive. The mysid swims constantly and shows no tendency for hanging motionless in the water. These observations are consistent with present hypotheses regarding the selective factors responsible for the low metabolic rates of deep-living pelagic species, and provide experimental evidence of reduced activity levels in deep-living animals.

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